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Behavioral Ecology

DOI:
10.1093/beheco/arz200

Published: 01/03/2020

Peer reviewed version

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Shannon, G., McKenna, M. F., Wilson-Henjum, G., Angeloni, L., Crooks, K., & Wittemyer, G. (2020). Vocal characteristics of prairie dog alarm calls across an urban noise gradient. *Behavioral Ecology*, *31*(2), 393-400. https://doi.org/10.1093/beheco/arz200

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04. May. 2023

Vocal characteristics of prairie dog alarm calls across an urban noise gradient

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Running title: Prairie dog alarm calls in noise

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Abstract

Increasing anthropogenic noise is having a global impact on wildlife, particularly due to the masking of crucial acoustical communication. However, there have been few studies examining the impacts of noise exposure on communication in free-ranging terrestrial mammals. We studied alarm calls of black-tailed prairie dogs (*Cynomys ludovicianus*) across an urban gradient to explore vocal adjustment relative to different levels of noise exposure. There was no change in the frequency 5%, peak frequency or duration of the alarm calls across the noise gradient. However, the minimum frequency – a commonly used, yet potentially compromised metric – did indeed show a positive relationship with noise exposure. We suspect this is a result of masking of observable call properties by noise, rather than behavioural adjustment. In addition, the proximity of conspecifics and the distance to the perceived threat (observer) did affect the frequency 5% of alarm calls. These results reveal that prairie dogs do not appear to be adjusting their alarm calls in noisy environments but likely do in relation to their social context and the proximity of a predatory threat. Anthropogenic noise can elicit a range of behavioural and physiological responses across taxa, but elucidating the specific mechanisms driving these responses can be challenging, particularly as these are not necessarily mutually exclusive. Our research sheds light on how prairie dogs appear to respond to noise as a source of increased risk, rather than as a distraction or through acoustical masking as shown in other commonly studied species (e.g. fish, songbirds, marine mammals).

Key words: acoustics, mammal, anthropogenic disturbance, communication, masking, predation

Introduction

Human-induced rapid environmental change is having far-reaching impacts on natural ecosystems across the globe, affecting animal behaviour, demographic processes and community composition (Sih et al. 2011). The pervasive nature of rising anthropogenic noise levels across terrestrial and aquatic habitats provides a prime example of how human activities can dramatically alter the environment over a comparatively short time frame (Barber et al. 2010). During the past two decades, increasing research effort has explored the effects of noise on animal behaviour and demography, with particular focus on how anthropogenic noise affects acoustic communication (Shannon, McKenna, et al. 2016).

Songbirds in particular have been the focus of numerous studies on the effects of anthropogenic noise on behaviour and communication in urban environments, due to their relative abundance, the important role of vocal communication in many aspects of their behaviour (e.g., territoriality, mate attraction and agonistic social interactions) and the established methodology for studying changes in song structure and singing behaviour (Slabbekoorn 2013). The seminal paper by Slabbekoorn and Peet (2003), which demonstrated that elevated noise levels in urban environments significantly altered vocal communication in great tits (*Parus major*), was a key catalyst for research effort on this topic. Scientists exploring avian acoustic communication have demonstrated a range of responses to mitigate the effects of noise exposure, which include adjusting the time of vocalising (Fuller et al. 2007), increasing the amplitude of the call (Lowry et al. 2012), lengthening the duration of the call (Díaz et al. 2011), reducing syllable rate (Potvin et al. 2011) and shifting the minimum call frequency upwards (Slabbekoorn and Ripmeester

2008). These behavioural adjustments are believed to be adaptive responses that reduce the masking of key signals by low frequency anthropogenic noise, which is predominantly concentrated at <2KHz (Brumm et al. 2017). Furthermore, evidence indicates that anthropogenic noise exposure may structure animal communities (Francis et al. 2009; Proppe et al. 2013), as species that vocalise at lower frequencies with limited behavioural flexibility are forced to adjust their distribution (Francis 2015). This suggests responses to noise are likely conditioned on the degree of plasticity in communication modalities.

Although the effects of anthropogenic noise on acoustic communication have been studied extensively across a range of taxa, including birds, marine mammals, amphibians and even invertebrates, there has been limited exploration of these effects in terrestrial mammals (Shannon, McKenna, et al. 2016). Terrestrial mammals display flexibility in call structures relative to social and geophysical conditions (Ey and Fischer 2009; Townsend and Manser 2013), and recent work has demonstrated that mongooses exhibit reduced responsiveness to conspecific and heterospecific vocalisations in road noise (Kern and Radford 2016; Morris-drake et al. 2017). However, studies explicitly exploring the effects of noise on vocalisations have largely been limited to research on bats. For example, Brazilian free-tailed bats (*Tadarida brasiliensis*) reduced the bandwidth of their echolocation search calls when exposed to noise (Bunkley and Barber 2015), fringe-lipped bats (*Trachops cirrhosus*) shifted from targeting prey-generated sources of sound to using echolocation when hunting in noise (Gomes et al. 2016), and Asian particolored bats (*Vespertilio sinensis*) simplified the complexity and raised the amplitude of their social calls when exposed to traffic noise (Jiang et al. 2019) but did not

93 adjust the vocal rate or duration of these vocalisations (Song et al. 2019). Other studies
94 have also explored shifts in frequency and amplitude of echolocating bats, but the
95 researchers exposed the animals to noise with a specific frequency (bandpass filtered),
96 compared with the broadband frequencies that are typical of anthropogenic noise (Hage
97 et al. 2013; Hage et al. 2014). The paucity of research on a wider range of mammal
98 species risks overlooking the impacts of a key anthropogenic stressor on terrestrial
99 systems.

100 In this paper, we explore whether a gradient of increasing urban traffic and
101 associated environmental noise affects the alarm call characteristics of black-tailed prairie
102 dogs (*Cynomys ludovicianus*) - hereafter referred to as prairie dogs. Prairie dogs are prey
103 species for a wide range of grassland predators including badgers (*Taxidea taxus*),
104 coyotes (*Canis latrans*), hawks and snakes (Hoogland 1995). Alarm calls – a series of
105 rapid high-pitched barks – provide one of the key anti-predator strategies employed by
106 this group-living species (Hoogland 1995), but the production of these calls appears to be
107 influenced by social context. For example, prairie dogs have been shown to give alarm
108 calls more readily when in the presence of kin compared to unrelated conspecifics
109 (Hoogland 1983; Hoogland 1995). This provides evidence that the seemingly costly
110 behaviour of an individual alerting a predator to their presence may have indirect fitness
111 benefits (Shelley and Blumstein 2005). Moreover, we recently demonstrated that the
112 presence of young influenced the alarm call characteristics of adult prairie dogs –
113 whereby they lowered the central concentration of energy in their calls (Wilson-Henjum
114 et al. 2019). The social context and function of alarm call production provides an
115 interesting avenue for exploring the effects of exposure to anthropogenic noise on animal

116 vocalisation, particularly when contrasted with findings from the significant body of
117 work focussing on advertisement calls and songs (reviewed by Shannon, McKenna, et al.
118 2016).

119 Although prairie dog populations across the United States have been dramatically
120 reduced as a result of land-use changes and disease (Miller, Ceballos, & Reading, 1994;
121 Miller et al., 2007), they have shown the ability to inhabit urban environments (Magle et
122 al. 2010; Magle and Fidino 2018). In common with other wildlife species that can survive
123 in human-dominated landscapes, this persistence is likely to be a function of their
124 behavioural flexibility, which allows them to adjust to the environmental conditions of
125 their surroundings (Lowry et al. 2013). Prairie dogs therefore provide an interesting study
126 species for furthering our understanding of behavioural and demographic responses to
127 anthropogenic disturbance in a social mammal. In addition to exploring vocal plasticity
128 relative to noise exposure in a free-ranging terrestrial mammal, this study also focuses on
129 a form of vocal communication that has received less attention in this field of research –
130 alarm calling to signal the presence of a perceived threat (Potvin et al. 2014; Templeton
131 et al. 2016). While calls and songs aimed at attracting mates and defending territories
132 play a crucial role in the reproductive success of an animal, alarm calls arguably have an
133 even more immediate and profound effect on fitness through the mediation of survival.

134 Our previous research found that prairie dogs exposed to noise adjusted their
135 vigilance and foraging behaviour, consistent with the risk disturbance hypothesis, which
136 predicts anthropogenic disturbance will elicit increased antipredator behaviour (Shannon
137 et al. 2014). Because of their enhanced vigilance, prairie dogs detected and responded to
138 an approaching predator quicker in noise than during the ambient control - contrary to the

distracted prey hypothesis (Shannon, et al., 2016). Here, we explore whether prairie dogs exhibit vocal plasticity in noise – a potential mechanism to overcome acoustical masking – to further illustrate how prairie dogs perceive and respond to this novel pollutant. This will not only broaden the types of communication studied in the context of increasing anthropogenic noise, but has implications for conserving animals in evolutionarily novel environments, such as urban areas that are dramatically expanding with human population growth. We predicted that prairie dogs would elevate the lower frequency limit of their alarm calls when exposed to increasing road traffic noise – so as to minimize acoustical masking.

Methods

Study sites

The study was conducted across three prairie dog colonies in predominantly shortgrass prairie habitat located within or adjacent to the city of Fort Collins, Colorado, USA. The sites were selected to provide a gradient of exposure to urban traffic and associated noise. Pineridge Natural Area (250 ha), located on the western edge of the city with a small country road on the northwest boundary (~750m from the center of the colony), experiences the least anthropogenic noise of the three colonies and is a site that we have used for previous research on prairie dog responses to road traffic noise (Shannon et al. 2016). Coyote Ridge Natural Area, situated close to the southwest boundary of the city, is 840 ha in extent and adjacent to a larger open space to the south and west; the center of the prairie dog colony is located ~350m from the relatively busy County Road 19. The Coterie Natural Area is a small (1.6 ha) site located within the city at the intersection of

two main roads (~50m to the center of the colony), resulting in considerable levels of urban noise. All three of the sites can be accessed by trails that are used by walkers, runners and cyclists. The prairie dogs are therefore regularly exposed to human activity.

Alarm call measurements

Prairie dog alarm calls were recorded from 28 August to 6 December 2014 using a Rode NTG-2 shotgun microphone, which was connected to a Roland Moore R-05 digital recorder. Data collection was carried out during daylight hours (0700 – 1900) by the same single observer (GWH). Alarm calls were elicited by the observer approaching a randomly selected prairie dog – with a systematic approach employed to ensure that different areas of the colony (and animals) were sampled from one study site visit to the next. Once the prairie dog began alarm calling the observer remained stationary and recorded 30 seconds of vocalization while the animal was in situ. Distance to the target animal and the distance from this individual to their nearest neighbor was measured using a laser range finder. All calls were recorded within a distance of 18m from the animal (mean ± SD = 9m ± 3) with small differences between sites (Pineridge = 10m ± 2, Coyote Ridge = 11m ± 3, The Coterie = 8m ± 2). In order to reduce the possibility that the same prairie dog was selected more than once during the same recording session, the observer ensured that there was a minimum of 30m (the average size of a burrow system; Sheets et al. 1971) between the individuals targeted for inclusion in the study. Wind speed and the prevailing weather conditions were all documented at the time of recording. A total of 137 alarm call recording periods were collected across the three sites (Pineridge = 46, Coyote Ridge = 44, The Coterie = 47).

A band-limited automated detector was used in Raven Pro v1.5 to select each of the individual barks in the 30-second calling bouts and to optimize extraction of call parameters. The following settings were used in the detector: minimum frequency of 2000 Hz, maximum frequency of 15000 Hz, minimum signal duration of 0.008 seconds, maximum signal duration of 0.2 seconds, minimum separation of 0.2 seconds, minimum occupancy of 30 percent, and a signal-to-noise threshold of 15 dB. Before measurements were extracted on the individual barks, all detections were examined manually for accuracy and adjusted to maximize the detection of all barks within a recording period and to ensure the entire bandwidth and duration of calls were selected. Because prairie dogs produce short duration, broadband barks, a standardized maximum frequency (15000 Hz) was used for each detection box. Random selections of half of the barks in a calling bout (n = 4516) were then measured.

Four acoustic metrics were calculated for each bark: (1) minimum frequency (Hz) – the lower frequency limit of the call, a commonly used metric in previous studies; (2) frequency 5% (Hz) – the frequency where the summed energy equals 5% of the total, a measure of lower frequency properties; (3) peak frequency (Hz) – the frequency with the highest concentration of energy; and (4) bark duration (milliseconds) (Figure 1).

Ambient sound level measurements

Ambient sound levels were measured using a calibrated Larson-Davis 831 sound level meter (frequency weighting = A) over a 2-minute period as soon as the vocalization recording was completed. Sound pressure levels were measured as 1-second frequency weighted (12.5Hz - 20kHz) equivalent continuous levels ($L_{Aeq, 1s}$). Although ambient

sound levels may fluctuate slightly from the time that the alarm call was recorded to the time that the sound pressure level was measured, we believe this variation was minimal relative to overall variation in ambient sound levels across sampling events and sites. Furthermore, it was not possible to conduct the measurements simultaneously, as the ambient sound level recordings would have been biased from the alarm call of the prairie dog. The sound pressure levels were downloaded with the SLM Utility-G3 and customized scripts in R were used to calculate the L_{Aeq} over 120 seconds associated with each recording period (see Electronic Supplementary Material for details).

Statistical analysis

To explore differences in prairie dog vocalisations across the three colonies, alarm call characteristics were initially analysed using a one-way ANOVA with Tukey's HSD. Response variables included the four acoustic metrics described above, and the analysis calculated the mean call characteristics for each target animal, averaged across multiple barks within a bout of alarm calling. The distribution of the residuals was plotted to check that the assumptions of the model were met (e.g., normality and homogeneity). To reduce the likelihood of type 1 errors with multiple comparisons of call parameters across sites, we used an alpha level of 0.01 to assess statistical significance.

Next, a generalized linear mixed model (GLMM) framework using the lme4 package in R (R Core Development Team 2019) was used to understand the conditions that correlate with changes in alarm call characteristics. Response variables included the four-acoustic metrics, and characteristics of each individual bark were entered into the analyses with the individual observation number included as a random effect to account

231 for the repeated measures (multiple barks) within a given alarm call. Akaike's
232 Information Criterion adjusted for small sample size (AICc) was used for model selection
233 (Burnham and Anderson 2002). A total of 29 candidate models were generated for each
234 of the response variables using combinations of five predictor variables (Table 1).
235 Predictor variables included the *ambient sound level* ($L_{Aeq,120s}$) when the calls bouts were
236 recorded, *Julian day* to establish if there was a change in response over the course of the
237 fieldwork, *distance recorded* to account for variation in the distance between the observer
238 and the target animal, *wind speed* to control for the influence of fluctuating acoustic
239 conditions, and *distance to the nearest neighbor* to determine if proximity to a
240 conspecific influences the observed alarm call response (Table 1). Two interactions were
241 also included to determine whether the effect of noise level exposure on acoustic
242 parameters was modulated by distance to the observer (*ambient sound level * distance*
243 *recorded*), and/or distance to the nearest prairie dog (*ambient sound level * distance to*
244 *the nearest neighbor*). These predictor variables were normalized so that the relative
245 contribution could be determined in the model averaged output (Table 2). The
246 AICcmodavg package was used to extract AICc scores and model weights for candidate
247 models of each response variable. Model averaging was conducted across models
248 accounting for ≥0.95 of the AICc weight to extract parameter β estimates and their 95%
249 confidence intervals (CI). The significance of the results was assessed by whether the
250 95% CI overlapped zero. This research was approved according to Colorado State
251 University Animal Care and Use Committee protocol 13-4112A.
252
253

Results

Pineridge Natural Area was the quietest of the three colonies with ambient sound levels of 26-50 dB $L_{Aeq,120s}$ (N = 46), mean = 36 dB ± 2 (95% CI), while Coyote Ridge experienced ambient sound levels of 34-54 dB $L_{Aeq,120s}$ (N = 45), mean = 42 dB ± 1 (95% CI) and The Coterie had the highest ambient sound levels 49-76 dB $L_{Aeq,120s}$ (N = 47), mean = 58 dB ± 2 (95% CI).

The minimum frequency of prairie dog alarm calls differed across the three colonies (ANOVA: $F_{2,134} = 8.703$, $P = 0.0003$); Pineridge had the lowest minimum frequency (mean = 1151 Hz ± 197 SD) followed by Coyote Ridge (1218 Hz ± 149 SD) and The Coterie (1297 Hz ± 161 SD: Figure 2a). The Tukey HSD test revealed a significant difference in minimum frequency between Pineridge and The Coterie ($P = 0.0002$), but not between Coyote Ridge and The Coterie ($P = 0.04$) and Pineridge and Coyote Ridge ($P = 0.22$). We did not detect significant differences across colonies for frequency 5% (ANOVA: $F_{2,134} = 1.694$, $P = 0.188$), peak frequency (ANOVA: $F_{2,134} = 1.442$, $P = 0.24$) or bark duration (ANOVA: $F_{2,134} = 1.648$, $P = 0.196$; Figure 2).

Minimum frequency of alarm calls was predicted by six top models, with three models contributing 63% of the AICc weight (Table 2). Ambient sound level ($L_{Aeq,120s}$) was a key parameter across these models, with increasing noise predicting elevated minimum frequency of alarm calls (Table 3). None of the other explanatory variables demonstrated a significant relationship with the minimum frequency of alarm calls (Table 3).

The frequency 5% call property was predicted by 10 top models, with three accounting for 54% of the AICc weight (Table 2). Ambient sound level ($L_{Aeq,120s}$) was not

277 a significant predictor, with little evidence that higher noise led to a lower frequency
278 alarm call (measured as frequency 5%) (Table 3). Frequency 5% was greater for alarm
279 calls recorded at distances further from the observer (Dist recorded) and when calling
280 prairie dogs were closer to the nearest neighbour (Dist Neighbor) (Table 3).
281 Peak frequency was predicted by 11 top models, of which three accounted for
282 50% of the AICc weight (Table 2). As with the analysis of frequency 5%, there was no
283 evidence of a clear relationship between the ambient sound level and the peak frequency
284 of the call (Table 3). Furthermore, no other variables were significant predictors of peak
285 frequency.
286 Bark duration was predicted by 7 top models, with three contributing 61% of the
287 AICc weight (Table 2). No explanatory variables had a significant relationship with bark
288 duration (Table 3).
289
290 **Discussion**
291 Alarm calls provide crucial information on the presence and proximity of predatory
292 threats – essential for prairie dogs, which are social prey species that are targeted by a
293 number of terrestrial and aerial predators (Hoogland 1995). As such, and in line with
294 previous research on a range of bird and marine mammal species (Shannon, McKenna, et
295 al. 2016), we predicted that prairie dogs would reduce the masking effect of urban noise
296 by increasing the lower frequency limit of their alarm calls when exposed to elevated
297 anthropogenic noise. The evidence for this, however, was limited. We did detect an
298 increase in the minimum frequency of alarm calls with increasing urban noise, but there
299 was no effect of urban noise on the frequency 5% metric, which is a more robust measure

300 of the minimum frequency of animal vocalisations (Brumm et al. 2017). Likewise, peak
301 frequency and bark duration of alarm calls were not related to ambient sound levels.
302 Previous studies have also shown that the frequency of bird vocalisations are not
303 consistently adjusted in urban noise across species (Hu and Cardoso 2010), and even
304 when they are modified, they can shift in the opposite direction to that predicted, i.e. with
305 lower frequency calls in noisier conditions potentially to increase transmission distance
306 (Potvin et al. 2014). For taxa with particularly low frequency calls, it may prove too
307 energetically costly (or physiologically challenging) to actually shift the frequency of
308 vocalisation high enough to reduce the risk of masking, while those that use higher
309 frequency calls are less affected by noise and therefore might not need to adjust their calls
310 (Hu and Cardoso 2010). Prairie dogs have short duration alarm calls that extend across a
311 broad range of frequencies from 1 kHz to >8 kHz, with a peak frequency of
312 approximately 3.5 kHz, while the energy in urban noise is generally focussed below 2.5
313 kHz. It may well be the case that the relatively high frequency of their vocalisations
314 means that prairie dogs do not experience significant masking from exposure to urban
315 noise.
316 While our findings of an increase in minimum frequency with rising noise level
317 concur with previous studies, scientists have recently questioned the methods used to
318 measure minimum frequency because they may result in false positives (Ríos-Chelén et
319 al. 2017; Brumm et al. 2017). Indeed, the majority of studies on this topic have relied on
320 researchers visually inspecting the spectrogram to determine the minimum vocal
321 frequency, a method that has been shown to potentially bias the results, particularly if the
322 observer has *a priori* expectations (Ríos-Chelén et al. 2017; Brumm et al. 2017).

323 Furthermore, the signal to noise ratio in acoustic data can result in the minimum
324 frequency being masked under elevated noise levels, resulting in artificial inflation of the
325 observed minimum frequency (Brumm et al. 2017). It was interesting to note the marked
326 difference in our model results for the minimum frequency and frequency 5% metrics,
327 further highlighting the risk of using the absolute minimum frequency when exploring
328 vocal adjustments by animals in anthropogenic noise.
329 We found evidence for changes in vocal behaviour related to the social context of the
330 alarm calls. Prairie dogs that were at a greater distance from conspecifics (i.e. more
331 isolated), and therefore may have been at a higher risk of predation, produced calls with
332 lower frequencies. We suggest that this could be a result of reduced call amplitude, which
333 is typically positively correlated with call frequency (Brumm and Naguib 2009; Zollinger
334 et al. 2012; Nemeth et al. 2013) – however it is important to note that we were unable to
335 measure alarm call amplitude in this study. Such a strategy of producing softer low-
336 amplitude calls, documented across a range of species, can reduce eavesdropping and
337 detection by a third-party (Reichard and Anderson 2015), in this case an approaching
338 predator in the form of a human observer. Prairie dogs also produced alarm calls with
339 increased lower frequencies when the observer (i.e., predator threat) was further from the
340 calling animal. Prairie dogs may elevate call amplitude, and consequently generate higher
341 frequency calls, when predators are at a greater distance to increase the likelihood the
342 vocalisation is received across a greater area of the colony, without unduly increasing the
343 risk to the caller. This is especially pertinent given that the function of the alarm call is to
344 both warn conspecifics of approaching danger and to communicate to the predator that
345 they have been detected (Isbell and Bidner 2016). Additional experiments conducted by

346 our research group demonstrated that prairie dogs adjusted their alarm calls – reducing
347 the central concentration of energy – when calling in the presence of vulnerable pups
348 (Wilson-Henjum et al. 2019). Adjustment in prairie dog communication, therefore,
349 appears to be structured by social context mediated by spatial proximity to an
350 approaching threat. However, this is an area of research that warrants further detailed
351 investigation to reveal the specific drivers of vocal modulation.
352 Unlike many previous studies that have explored the effects of anthropogenic
353 noise on communication, our research focussed on alarm calls rather than songs or
354 vocalisations that animals use to advertise their quality or fitness to conspecifics
355 (reviewed in Shannon, McKenna, et al. 2016). The effective communication distance for
356 an alarm call in a colonial species may be significantly less than that of a call or song
357 aimed at attracting a mate or defending a territory. Therefore, even though the ambient
358 noise levels were considerable (mean of 58 dB at the Coterie, which is comparable to
359 normal conversation at 1m), they may not be loud enough to sufficiently mask the alarm
360 call from being perceived by nearby conspecifics. This raises a number of interesting
361 future research avenues regarding the function of a given vocalisation and its
362 susceptibility to masking from anthropogenic noise, as well as the plasticity in response
363 exhibited across taxa. It is also important to note that practical limitations meant that we
364 only had three sites in our study design, each with a different noise exposure resulting in
365 some level of pseudoreplication. Ideally, further research on this topic will identify
366 multiple sites at each broad level of noise exposure.
367 Elucidating the specific mechanisms (e.g., distraction, masking, predatory threat,
368 social context) driving behavioural responses to anthropogenic noise can prove

challenging, particularly as they are not necessarily mutually exclusive. Nevertheless, a combination of natural experiments and playback approaches can be used to identify the key mechanisms for specific taxa, which can greatly inform our understanding of the effects of noise, as well as assist in developing effective mitigation of these impacts (Francis and Barber 2013). Our work on free-ranging prairie dogs has demonstrated that they adjust critical behaviours when exposed to noise – including increased vigilance and reduced foraging – which suggests that noise is responded to as an elevated level of perceived risk (Shannon et al. 2014). Furthermore, in contrast to a number of aquatic species (Chan et al. 2010; Wale et al. 2013; Simpson et al. 2015), prairie dogs did not exhibit distraction from an approaching predator under noisy conditions – indeed, they actually became alert and took flight sooner in traffic noise than under quieter control conditions (Shannon et al. 2016). While the findings presented here suggest that the acoustic characteristics of prairie dog alarm calls are consistent across a broad range of ambient noise levels, indicating that masking may not be a key driver shaping their vocal behaviour under these conditions.

Funding

The National Park Service Natural Sounds and Night Skies Division funded this research.

Acknowledgements

We would like to thank J. Shanahan and A. Meyer at Fort Collins Natural Areas for logistical support and permission to conduct the study, and L. Cordes for statistical advice.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Shannon et al. (2019).

References

Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25:180–189.

Brumm H, Naguib M. 2009. Environmental Acoustics and the Evolution of Bird Song. In: M Naguib, K, Zuberbuhler, NS Clayton VJ, editor. Advances in the Study of Behavior. Vol. 40. Academic Press. p. 1–33.

Brumm H, Zollinger SA, Niemelä PT, Sprau P. 2017. Measurement artefacts lead to false positives in the study of birdsong in noise. Methods Ecol. Evol. 11:1617–1625.

Bunkley JP, Barber JR. 2015. Noise Reduces Foraging Efficiency in Pallid Bats (*Antrozous pallidus*). Ethology 121:1116–1121.

Burnham K, Anderson D. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Chan AAY-H, Giraldo-Perez P, Smith S, Blumstein DT. 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biol. Lett. 6:458–461.

Díaz M, Parra A, Gallardo C. 2011. Serins respond to anthropogenic noise by increasing vocal activity. Behav. Ecol. 22:332–336.

Ey E, Fischer J. 2009. The "Acoustic adaptation hypothesis" - A review of the evidence from birds, anurans and mammals. Bioacoustics 19:21–48.

Francis CD. 2015. Vocal traits and diet explain avian sensitivities to anthropogenic noise. Glob. Chang. Biol. 21:1809–1820.

Francis CD, Barber JR. 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. Front. Ecol. Environ. 11:305–313.

Francis CD, Ortega CP, Cruz A. 2009. Noise Pollution Changes Avian Communities and Species Interactions. Curr. Biol. 19:1415–1419.

Fuller RA, Warren PH, Gaston KJ. 2007. Daytime noise predicts nocturnal singing in

422 urban robins. Biol. Lett. 3:368–70.
423 Gomes DGE, Page RA, Geipel I, Taylor RC, Ryan MJ, Halfwerk W. 2016. Bats
424 perceptually weight prey cues across sensory systems when hunting in noise.
425 Science 353:1277–1280.
426 Hage S, Jiang T, Berquist S, Feng J, Metzner W. 2013. Ambient noise induces
427 independent shifts in call frequency and amplitude within the Lombard effect in
428 echolocating bats. Proc. Natl. Acad. Sci. 110:4063–4068.
429 Hage SR, Jiang T, Berquist SW, Feng J, Metzner W. 2014. Ambient noise causes
430 independent changes in distinct spectro-temporal features of echolocation calls in
431 horseshoe bats. J. Exp. Biol. 217:2440–4.
432 Hoogland JL. 1983. Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys*
433 *ludovicianus*). Anim. Behav. 31:472–479.
434 Hoogland JL. 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal.
435 University of Chicago Press.
436 Hu Y, Cardoso GC. 2010. Which birds adjust the frequency of vocalizations in urban
437 noise? Anim. Behav. 79:863–867.
438 Isbell LA, Bidner LR. 2016. Vervet monkey (*Chlorocebus pygerythrus*) alarm calls to
439 leopards (*Panthera pardus*) function as a predator deterrent. Behaviour 153:591–
440 606.
441 Jiang T, Guo X, Lin A, Wu H, Sun C, Feng J, Kanwal JS. 2019. Bats increase vocal
442 amplitude and decrease vocal complexity to mitigate noise interference during
443 social communication. Anim. Cogn. 22:199–212.
444 Kern JM, Radford AN. 2016. Anthropogenic noise disrupts use of vocal information
445 about predation risk. Environ. Pollut. 218:988–995.
446 Lowry H, Lill A, Wong BBM. 2012. How Noisy Does a Noisy Miner Have to Be?
447 Amplitude Adjustments of Alarm Calls in an Avian Urban 'Adapter.' PLoS One
448 7:e29960.
449 Lowry H, Lill A, Wong BBM. 2013. Behavioural responses of wildlife to urban
450 environments. Biol. Rev. 88:537–549.
451 Magle SB, Fidino M. 2018. Long-term declines of a highly interactive urban species.
452 Biodivers. Conserv. 27:3693–3706.

453 Magle SB, Reyes P, Zhu J, Crooks KR. 2010. Extirpation, colonization, and habitat
454 dynamics of a keystone species along an urban gradient. Biol. Conserv. 143:2146–
455 2155.
456 Miller B, Ceballos G, Reading R. 1994. The prairie dog and biotic diversity. Conserv.
457 Biol. 8:677–681.
458 Miller BJ, Reading RP, Biggins DE, Detling JK, Forrest SC, Hoogland JL, Javersak J,
459 Miller SD, Proctor J, Truett J, et al. 2007. Prairie Dogs: An Ecological Review and
460 Current Biopolitics. J. Wildl. Manage. 71:2801–2810.
461 Morris-drake A, Bracken AM, Kern JM, Radford AN. 2017. Anthropogenic noise alters
462 dwarf mongoose responses to heterospecific alarm calls. Environ. Pollut. 223:476–
463 483.
464 Nemeth E, Pieretti N, Zollinger SA, Geberzahn N, Partecke J, Brumm H, Miranda AC.
465 2013. Bird song and anthropogenic noise : vocal constraints may explain why birds
466 sing higher-frequency songs in cities. Proc. R. Soc. B Biol. Sci. 280:20122798.
467 Potvin DA, Mulder RA, Parris KM. 2014. Silvereyes decrease acoustic frequency but
468 increase efficacy of alarm calls in urban noise. Anim. Behav. 98:27–33.
469 Potvin DA, Parris KM, Mulder RA. 2011. Geographically pervasive effects of urban
470 noise on frequency and syllable rate of songs and calls in silvereyes (*Zosterops*
471 *lateralis*). Proc. Biol. Sci. 278:2464–9.
472 Proppe DS, Sturdy CB, St. Clair CC. 2013. Anthropogenic noise decreases urban
473 songbird diversity and may contribute to homogenization. Glob. Chang. Biol.
474 19:1075–1084.
475 R Core Development Team. 2019. R: a language and environment for statistical
476 computing. Vienna (Austria): R Foundation for Statistical Computing.
477 Reichard DG, Anderson RC. 2015. Why signal softly? The structure, function and
478 evolutionary significance of low-amplitude signals. Anim. Behav. 105:253–265.
479 Ríos-Chelén AA, McDonald AN, Berger A, Perry AC, Krakauer AH, Patricelli GL. 2017.
480 Do birds vocalize at higher pitch in noise, or is it a matter of measurement? Behav.
481 Ecol. Sociobiol. 71:1–12.
482 Shannon G, Angeloni LM, Wittemyer G, Fristrup KM, Crooks KR. 2014. Road traffic
483 noise modifies behaviour of a keystone species. Anim. Behav. 94:135–141.

484 Shannon G, Crooks KR, Wittemyer G, Fristrup KM, Angeloni LM. 2016. Road noise
485 causes earlier predator detection and flight response in a free-ranging mammal.
486 Behav. Ecol. 27:1370–1375.
487 Shannon G, McKenna MF, Angeloni LM, Crooks KR, Fristrup KM, Brown E, Warner
488 KA, Nelson MD, White C, Briggs J, et al. 2016. A synthesis of two decades of
489 research documenting the effects of noise on wildlife. Biol. Rev. 91:982–1005.
490 Shannon G, McKenna MF, Wilson-Henjum GE, Angeloni LM, Crooks KR, Wittemyer
491 G. 2019. Data from: Vocal characteristics of prairie dog alarm calls across an urban
492 noise gradient. Behav. Ecol. doi: https://doi.org/10.5061/dryad.vmcvdncp9
493 Sheets RG, Linder RL, Dahlgren RB. 1971. American Society of Mammalogists Burrow
494 Systems of Prairie Dogs in South Dakota. Source J. Mammal. 52:451–453.
495 Shelley EL, Blumstein DT. 2005. The evolution of vocal alarm communication in
496 rodents. Behav. Ecol. 16:169–177.
497 Sih A, Ferrari MCO, Harris DJ. 2011. Evolution and behavioural responses to human-
498 induced rapid environmental change. Evol. Appl. 4:367–387.
499 Simpson SD, Purser J, Radford AN. 2015. Anthropogenic noise compromises
500 antipredator behaviour in European eels. Glob. Chang. Biol. 21:586–593.
501 Slabbekoorn H. 2013. Songs of the city: noise-dependent spectral plasticity in the
502 acoustic phenotype of urban birds. Anim. Behav. 85:1089–1099.
503 Slabbekoorn H, Ripmeester EAP. 2008. Birdsong and anthropogenic noise: implications
504 and applications for conservation. Mol. Ecol. 17:72–83.
505 Song S, Lin A, Jiang T, Zhao X, Metzner W, Lin A, Feng J. 2019. Bats adjust temporal
506 features of echolocation calls but not those of communication calls in response to
507 traffic noise. Integr. Zool.
508 Templeton CN, Zollinger SA, Brumm H. 2016. Traffic noise drowns out great tit alarm
509 calls. Curr. Biol. 26:R1173–R1174.
510 Townsend SW, Manser MB. 2013. Functionally Referential Communication in
511 Mammals : The Past , Present and the Future. 119:1–11.
512 Wale M a., Simpson SD, Radford AN. 2013. Noise negatively affects foraging and
513 antipredator behaviour in shore crabs. Anim. Behav. 86:111–118.
514 Wilson-Henjum GE, Job JR, McKenna MF, Shannon G, Wittemyer G. 2019. Alarm call

modification by prairie dogs in the presence of juveniles. J. Ethol. 37:167–174.

Zollinger SA, Podos J, Nemeth E, Goller F, Brumm H. 2012. On the relationship between, and measurement of, amplitude and frequency in birdsong. Anim. Behav. 84:e1–e9.

Figure legends

Figure 1. Spectrogram of black-tailed prairie dog alarm calls collected from the colony at The Coterie Natural Area. The extracted call parameters are shown for a single call. Spectrogram parameters: 512 fast Fourier transformation, Hann window, 50% overlap, 93-Hz frequency resolution, 3.25 ms temporal resolution. The dark band of energy below 2.5 kHz is generated by urban noise at the study site.

Figure 2. Mean (± 95% CI) values for the four acoustic metrics extracted from prairie dog calls (n = 137) across the three study sites with increasing noise exposure from left to right.

Table 1. Structure of candidate models assessed for the four response variables (minimum frequency, frequency 5%, peak frequency and bark duration). Individual observation number was included as a random effect.

Null
Sound level
Wind speed
Julian day
Dist recorded
Dist neighbor
Sound level + Wind speed
Sound level + Julian day
Sound level + Dist recorded
Sound level + Dist neighbor
Julian day + Wind speed
Julian day + Dist recorded
Julian day + Dist neighbor
Dist recorded + Dist neighbor
Dist neighbour + Wind speed
Sound level + Julian day + Wind speed
Sound level + Julian day + Dist recorded
Sound level + Julian day + Dist neighbour
Sound level + Dist recorded + Wind speed
Julian day + Dist recorded + Wind speed
Julian day + Dist recorded + Dist neighbor
Wind speed + Dist recorded + Dist neighbor
Sound level + Windspeed + Dist recorded + Dist neighbor
Sound level + Dist neighbour + Dist recorded + Julian Day
Sound level + Windspeed + Dist recorded + Julian Day
Wind speed + Dist neighbour + Dist recorded + Julian Day
Sound level + Julian day + Wind speed + Dist recorded + Dist neighbor
Sound level * Dist recorded
Sound level * Dist Neighbor

570 **Table 2.** Top models for the four-acoustic metrics of prairie dog alarm calls (≥0.95 of the

571 AICc weight). All models include the individual observation number as a random effect.

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	K	ΔAICc	AICc weight
a) **Minimum frequency**			
Sound level + Dist recorded + Julian Day + Dist neighbor	7	0.00	0.29
Sound level * Dist neighbor	6	0.84	0.19
Sound level + Dist neighbor	5	1.24	0.15
Sound level + Dist recorded + Dist neighbour + Wind speed	7	1.54	0.13
Sound level + Dist recorded + Julian Day + Dist neighbor + Wind speed	8	1.70	0.12
Sound level + Julian Day + Dist neighbor	6	1.92	0.11
a) **Frequency 5%**			
Dist recorded + Dist neighbor	5	0.00	0.25
Julian Day + Dist recorded + Dist neighbor	6	1.12	0.15
Wind speed + Dist recorded + Dist neighbor	6	1.12	0.14
Dist recorded + Dist neighbor + Julian Day + Wind speed	7	2.11	0.09
Dist neighbor	4	2.59	0.07
Sound level + Dist recorded + Julian Day + Dist neighbor	7	2.78	0.06
Sound level + Dist recorded + Dist neighbor + Wind speed	7	2.90	0.06
Dist neighbor + Wind speed	5	3.48	0.05
Sound level + Dist recorded + Julian Day + Dist neighbor + Wind speed	8	3.71	0.04
Julian Day + Dist neighbor	5	3.81	0.04
b) **Peak frequency**			
Dist neighbour	4	0.00	0.19
Dist recorded * Dist neighbor	6	0.27	0.16
Dist recorded + Dist neighbor	5	0.49	0.15
Dist neighbor + Wind speed	5	1.12	0.11
Sound level + Dist neighbor	5	1.71	0.08
Wind speed + Dist recorded + Dist neighbor	6	1.75	0.08
Julian day + Dist neighbor	5	2.00	0.07
Julian day + Dist recorded + Dist neighbor	6	2.50	0.05
Sound level + Julian day + Dist neighbor	6	3.70	0.03
Wind speed + Dist neighbor + Dist recorded + Julian Day	7	3.76	0.03
Sound level + Windspeed + Dist recorded + Dist neighbor	7	3.76	0.03

c) **Bark duration**			
Dist neighbor	4	0.00	0.28
Julian day + Dist neighbor	5	1.03	0.17
Sound level + Dist neighbor	5	1.04	0.16
Dist recorded + Dist neighbor	5	1.75	0.12
Sound level + Julian Day + Dist neighbor	6	2.27	0.09
Sound level * Dist neighbor	6	2.32	0.09
Julian day + Dist recorded + Dist neighbor	6	2.76	0.07

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589 **Table 3.** The observed relationship between each response variable and the model-
590 averaged parameters from the top models (β-estimate ±95% CI). Bold text denotes β-
591 estimates with 95% CI that do not overlap zero.
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	Parameter	β Estimate	(95% CI)
Minimum frequency	Sound level	**67.63**	**(20.18 / 115.09)**
	Dist recorded	44.16	(-0.27 / 88.58)
	Dist neighbor	8.10	(-33.65 / 49.85)
	Julian day	25.29	(-13.03 / 63.60)
	Wind speed	-1.27	(-6.26 / 3.72)
	Sound level * Dist neighbor	-40.89	(-92.22 / 10.44)
Frequency 5%	Sound level	17.02	(-100.00 / 134.04)
	Dist recorded	**125.31**	**(11.3 / 239.31)**
	Dist neighbor	**-144.57**	**(-258.96 / -30.18)**
	Julian day	52.54	(-52.68 / 157.76)
	Wind speed	-6.93	(-20.72 / 6.86)
Peak frequency	Sound level	-50.22	(-176.87 / 76.43)
	Dist recorded	69.38	(-44.69 / 183.46)
	Dist neighbor	-45.05	(-159.71 / 69.61)
	Julian day	-2.74	(-109.24 / 103.77)
	Wind speed	-6.38	(-20.29 / 7.53)
	Sound level * Dist neighbor	-134.37	(-274.70 / 5.96)
Bark duration	Sound level	0.91	(-1.39 / 3.22)
	Dist recorded	-0.55	(-3.08 / 1.98)
	Dist neighbor	0.12	(-2.37 / 2.61)
	Julian day	-1.13	(-3.44 / 1.18)
	Wind speed	-0.02	(-0.33 / 0.28)
	Sound level * Dis neighbor	-1.34	(-4.43 / 1.74)

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